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ORIGINAL RESEARCH

Humulus japonicus Accelerates the Decomposition of *Miscanthus sacchariflorus* and *Phragmites australis* in a Floodplain

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Abstract *Humulus japonicus* in communities of *Miscanthus sacchariflorus* and *Phragmites australis* can grow large enough to overtop other species in the Amsa-dong floodplain. Because of strong winds and the weight of *Humulus*, plants of *M. sacchariflorus* and *P. australis* fell in mid-August and were subject to decomposition under its dense shading. To assess the effects of *H. japonicus* on nutrient cycling in these communities, we collected fresh samples of *M. sacchariflorus* and *P. australis* in litterbags and decomposed them under *H. japonicus* for 9 months, beginning in August. Biomass and organic contents from *M. sacchariflorus* during this incubation period were 49–51% and 44–48%, whereas those of *P. australis* were 49–61% and 32–52%, respectively. Their annual *k* values were 1.61–1.74 and 1.46–3.54, respectively. Initial N concentrations in *M. sacchariflorus* and *P. australis* were 13 and 20 mg g^{-1}, while C:N ratios were 31 and 21, respectively. These results indicate that *H. japonicus* is responsible for the collapse of *M. sacchariflorus* and *P. australis* in August and also accelerates their nutrient cycling through rapid decomposition, thereby increasing nutrient circulation in floodplains.

Keywords Change in nutrients · C:N ratio · Decay constant · *Humulus japonicus* · Riverine wetlands

Wetlands are defined as regions of shallow water covered by emergent herbaceous vegetation, such as reeds, cattails, wild rice, and rushes (Hammer 1995; Mun et al. 2000). Their productivity, as well as the diversity of wild annual species and other plants, is high in floodplains, where communities have a sufficient water supply and enhanced nutrient inputs from the surrounding lands. However, the structure and function of these unique communities in Korea have been destroyed by invasive plants, such as *Humulus japonicus* S. et Z. and *Sicyos angulatus* L. (Seoul City 2003).

Rapidly growing, *H. japonicus* is an aggressive annual vine with double- or single-hooked climbing hairs (Ehara 1955; Ju et al. 2006). It originated in South Asia, spread widely in tropical and subtropical zones (Bae 2000), and was introduced into Korea a long time ago (Lee 1980). Seeds germinate under *Miscanthus sacchariflorus* and *Phragmites australis* in May, but by August, *Humulus* seedlings overtop these other species in riverine wetlands. Where winds are strong, plants of *M. sacchariflorus* and *P. australis* cannot withstand the weight of *H. japonicus* overhead, so they fall and become completely covered by the latter. Growth of other plants is impossible under *H. japonicus* because of deficient light (Seoul City 2001), and these floodplains soon comprise only *H. japonicus*. This significantly changes the unique structure and function of those riverine wetlands, especially with respect to animal habitat and landscape.

We previously reported on how *H. japonicus* affects nutrient cycling in communities where it dominates (Kim et al. 2006), but that research focused solely on the influence of naturally dried *Humulus.* Therefore, the objectives of this current study were to (1) measure the decomposition rates of *M. sacchariflorus* and *P. australis* under *H. japonicus* from the middle of August, (2) compare these data with those obtained beginning in October, when *M. sacchariflorus* and *P. australis* are naturally withered (Kim et al. 2006), and (3) reveal how much *H. japonicus* accelerates this decomposition process. Our goal was to understand the mechanism by which *H. japonicus* grows rapidly and accelerates nutrient cycling in riverine wetlands.

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Materials and Methods

Study Area

This study was done on a floodplain of Han-gang River near the Amsa-dong Ecosystem Preservation Area, Seoul, Korea (37°33′N, 127°07′E). This area was formed naturally through sediment accumulation and is flat with little slope. Although plant communities of *P. australis*, *M. sacchariflorus*, and *Salix pseudolasiogyne* originally flourished in this area, *H. japonicus* became dominant by 2004, comprising 40% of the region (Seoul City 2005). The annual mean temperature and mean precipitation for 2004 to 2007 were 13°C and 1,440 mm. Monthly mean temperatures for August, September, and October of 2007 were 26.5°C, 21.5°C, and 15.1°C (Fig. 1), respectively, and no flooding was reported there between August 2006 and May 2007. Soil water contents ranged from 28% to 51% during the summer.

Litterbag Preparation

Live plants of *M. sacchariflorus* and *P. australis* were collected in mid-August 2006, and were separated into leaf and stem portions. Litterbags (20×20 cm) were filled with 25 g of fresh leaves and 25 g of fresh stems, the normal ratio in nature. Two mesh sizes (1 and 5 mm) litterbags were utilized, and each litterbag contained only one species.

Litterbag Retrieval and Chemical Analyses

Four replicates of our four bag types (two mesh sizes × two species) were retrieved at 0, 1, 3, 5, 9, 15, and 38 weeks after they were installed under a closed canopy of *H. japonicus* on the upper, flat part of the floodplain. Samples were dried at 60°C for more than 48 h after materials adhering to the bag exteriors were removed. The dried samples were then ground in a Willy Mini-Mill (3380L10, THOMAS, USA) and passed through a standard No. 40 sieve.

Chemical analyses of subsamples were conducted to identify the components of this organic matter following combustion at 550°C for 4 h in a muffle furnace (Dean 1974; Boyle 2004). To determine the concentrations of Na, Ca, K, Mg, and P, we mixed 0.5 g of sample powder with 5 ml of nitric acid and 1 ml of peroxide and acid-digested them with a microwave (MarsXpress, CEM, USA). An atomic absorption spectrophotometer (240FS, Varian, USA) was used to examine the major cations in these digested solutions. Phosphorus was measured according to the ammonium molybdate–sulfuric acid method (Mosse et al. 2006). Total C and N were determined with an element analyzer (EA1110, CE Instrument, Italy) at the National Center for Inter-University Research Facilities (NCIRF) at Seoul National University.

The remaining weight of the litter was depicted as a percentage of the initial sample weight based on dry mass.

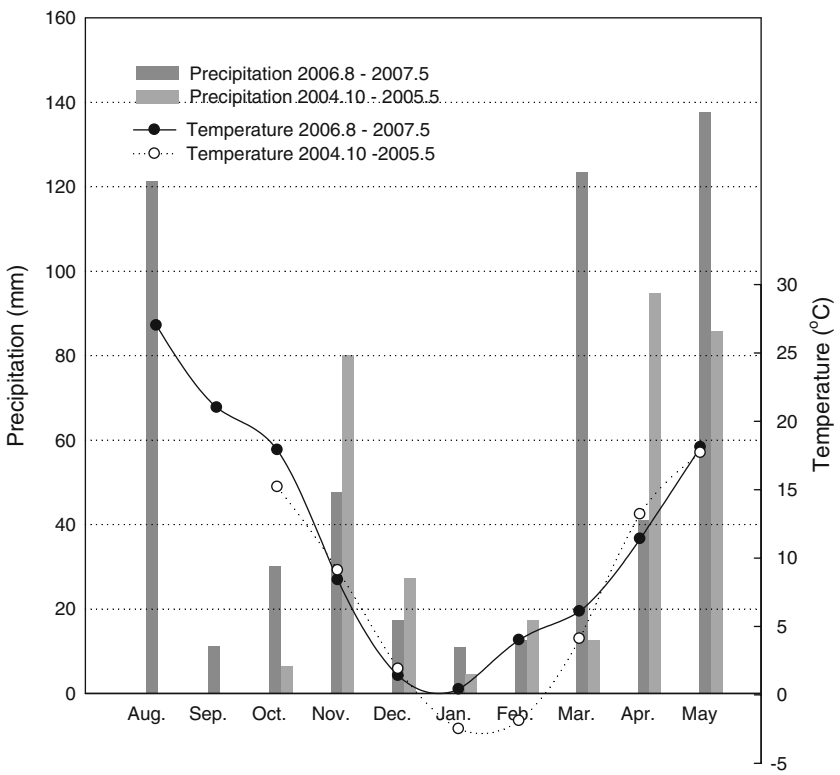

Fig. 1 Monthly mean temperature and precipitation in Seoul from October 2004 to May 2005 and from August 2006 to May 2007. Data from Korea Meteorological Administration

Decomposition rates (k) were determined from a single negative exponential model ($Mt = M_o \times e^{-kt}$, where Mo is the dry mass at t=0, and Mt is the dry mass at time t; Kim 2001). SPSS (version 10) and SigmaPlot (SPSS, Inc. version 10) were used for the statistical analyses.

Results and Discussion

Decomposition Rate

Dry masses in the litterbags decreased dramatically for the first 60 days, after which, this decline slowed considerably (Fig. 2). After 60 days, values for *M. sacchariflorus* and *P. australis* were 60% and 62% of the original, respectively, in the 1-mm bags, while those in the 5-mm bags were 54% and 51%, respectively. Over 263 days, the remaining dry masses of *M. sacchariflorus* and *P. australis* were 51% and 61% in the 1-mm bags and 49% and 49% in the 5-mm bags, respectively, compared with their original weights.

We have previously shown that the decomposition of *M. sacchariflorus* and *P. australis* under natural withering conditions produces dry mass values of 76% and 69% (1-mm mesh) and 80% and 76% (5-mm mesh), respectively, in the first 50 days (Kim et al. 2006). Therefore, the current data demonstrate that decomposition of these two species is accelerated when they are overtopped by *H. japonicus*.

We have also reported that the decomposition pattern of plant material generally can be divided into three phases: initially rapid weight loss, an extended period of active microbial decomposition, and then very slow decomposition of refractory compounds (Kim 2001). That first phase is caused by the leaching of soluble components. Here, the rapid loss of mass might have resulted from leaching and mineralization by microbes, which possibly occurred because fresh plant materials were used here rather than air-dried tissues in our earlier research (see Kim et al. 2006). Generally, this use of fresh samples (see van der Valk and Attiwill 1984; Valiela et al. 1984; Hemminga et al. 1988; Pozo and Colino 1992; Wrubleski et al. 1997) leads to fairly high leaching losses compared with the tests on dead material (see Hackney and de la Cruz 1980; Buth 1987; Wrubleski et al. 1997). In addition, high plant-moisture contents and seasonal factors, i.e., high temperature and humidity, could have stimulated microbial activity and promoted greater rates of decomposition.

After October, decay progressed more slowly because plants in the litterbags were then nearly completely desiccated and the weather was drier and colder. Likewise, although the weather became warm and very humid beginning in March of the following year, the process of decomposition slowed to the level described previously for naturally withered plants. This indicated that the final phase had begun, in which degradation of remaining recalcitrant materials is deterred (Swift et al. 1979).

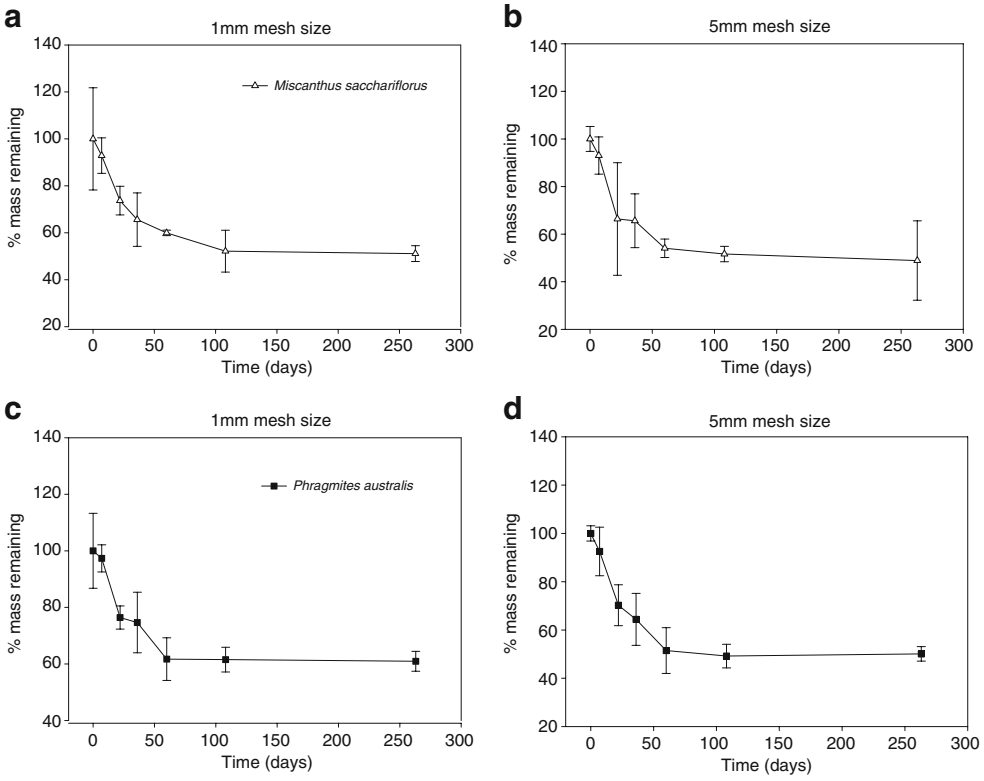

Fig. 2 Changes in dry mass of decaying *Miscanthus sacchariflorus* and *Phragmites australis* over time in litterbags with mesh sizes of 1 mm (**a**, **c**) and 5 mm (**b**, **d**; mean±1 SD, n=3 or 4)

Table 1 Annual decomposition rates, k (year^{-1}, mean ± SE, n=4) and decay time (years)

Plants	Site[e]	k value	Half-life	Reference
M[a]1[b]	Amsa-dong	1.740±0.61	0.398	This study
M1	Amsa-dong	1.83	0.379	Kim et al. 2006
M5[c]	Amsa-dong	1.611±0.57	0.430	This study
M5	Amsa-dong	2.16	0.321	Kim et al. 2006
M	Lake Paldangho	0.567	1.222	Shim et al. 1996
P[d]1	Amsa-dong	1.460±0.50	0.475	This study
P1	Amsa-dong	1.18	0.587	Kim et al. 2006
P5	Amsa-dong	3.536±1.07	0.196	This study
P5	Amsa-dong	0.02	35	Kim et al. 2006
P	Lake Paldangho	0.826	0.839	Shim et al. 1996

[a] *Miscanthus sacchariflorus*

[b] In 1-mm mesh bag

[c] In 5-mm mesh bag

[d] *Phragmites australis*

[e] Amsa-dong and Lake Paldangho are in Korea

Per-annum decay constants (k) for *M. sacchariflorus* and *P. australis* were 1.76 and 1.46 in the 1-mm mesh and 1.61 and 3.54 in the 5-mm mesh, respectively. These values did not differ statistically between bag's mesh sizes. Half-lives for *M. sacchariflorus* and *P. australis* were 0.40 and 0.48 year (1 mm) and 0.43 and 0.20 year (5 mm), respectively. Compared with earlier studies, our k values were much larger and half-lives much shorter (Table 1). The difference in mesh sizes had no effect on the functions of microbes and macro-invertebrates (cf., Kim et al. 2006), meaning that the former had a much more important role than did the latter in plant decomposition within this riverine ecosystem.

The moisture contents in plants of *M. sacchariflorus* and *P. australis* in August that had collapsed under the *Humulus* were 67.0–78.4 and 66.5–73.4%, respectively, compared with values of 30.5–65.2 and 38.4–59.1%, respectively, at the end of October, when plants were naturally withered (Fig. 3). These high contents in August might have accelerated decomposition. Godshalk and Wetzel (1978) and Swift et al. (1979) have suggested that both environmental factors and the quality of litter can greatly affect decay rates. Here, the major environmental variables probably included both moisture levels and temperature (Figs. 1 and 3). The importance of C:N ratios for the mineralization of biological materials has been emphasized by Cotrufo et al. (1994) and Mckane et al. (1997). Moreover, Zang and Zak (1995) have demonstrated that a low C:N ratio and a high amount of N are correlated with greater microbial activity and faster decomposition. Smith and Smith (2001) have found that the immobilization of nitrogen continues to a C:N ratio of 15–30 before mineralization starts. In our current study, ratios within *M. sacchariflorus* and *P. australis* ranged between 20–38 and 20–30, respectively (Fig. 4), indicating that their decomposition was caused by a constant state of mineralization and microbial activity. For naturally withering *Miscanthus*, the C:N ratio is 32–62 (Kim et al. 2006). Therefore, these differences in ratios might have been a factor responsible for the conflicting rates of decay between the current research and our earlier study (Kim et al. 2006).

Changes in Nutrient Contents

Nitrogen concentrations did not differ significantly between the 1- and 5-mm mesh sizes (Table 2). Initial N values from *M. sacchariflorus* and *P. australis* were 13 and 20 mg g^{-1},

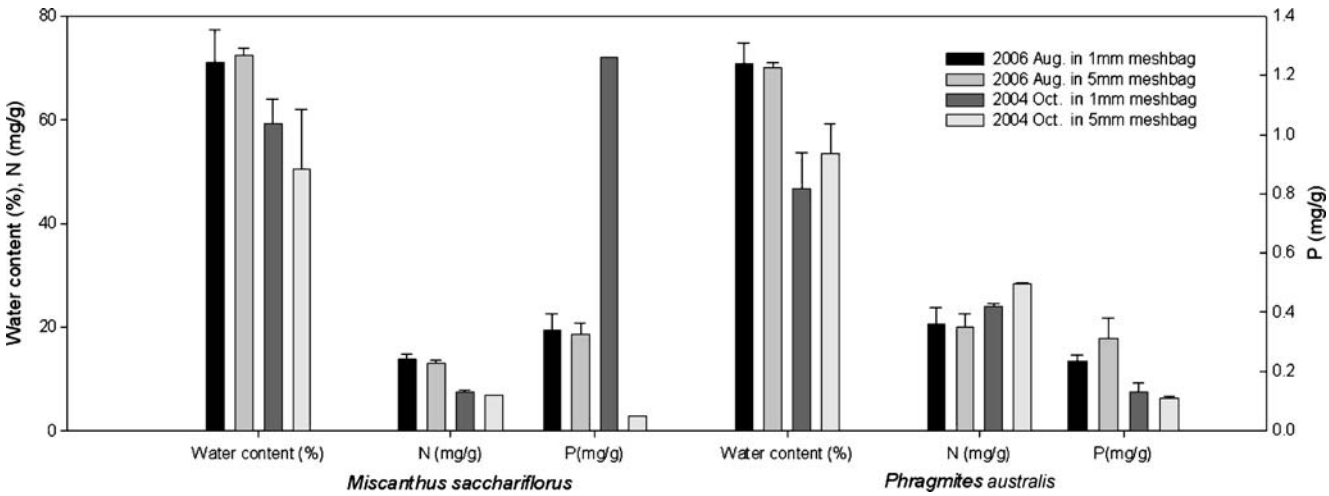

Fig. 3 Moisture contents (%), initial N (mg g^{-1}), and initial P (mg g^{-1}) within decaying *Miscanthus sacchariflorus* and *Phragmites australis* (mean±1 SD, n=3 or 4)

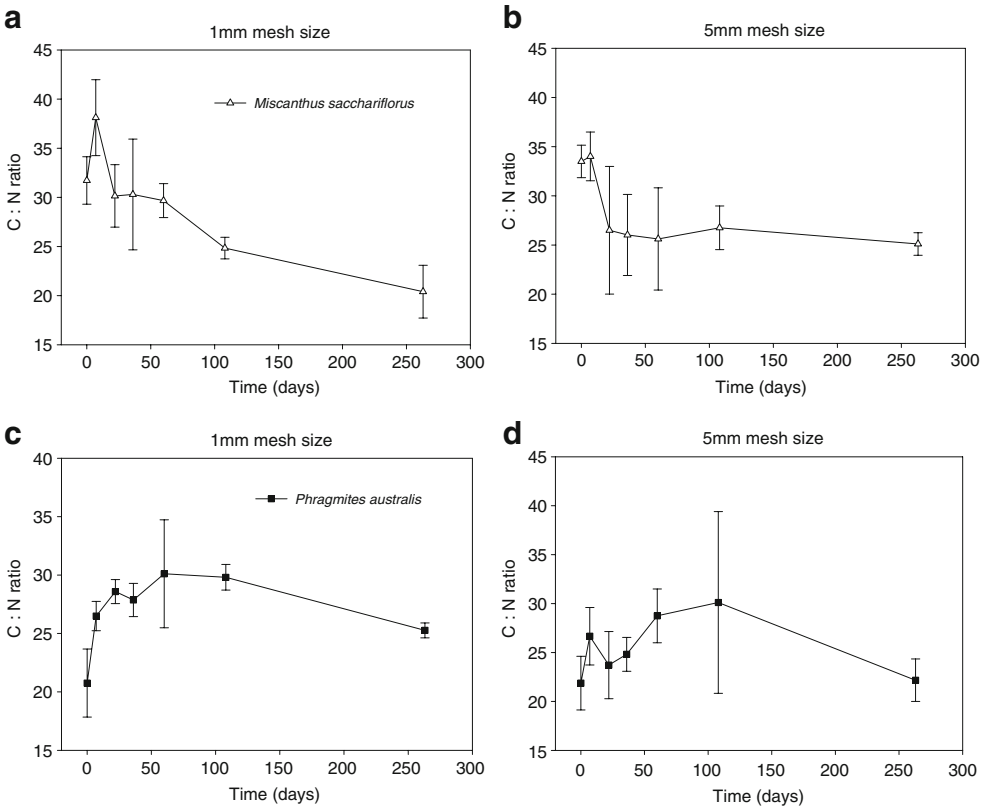

Fig. 4 Changes in C:N ratio from decaying *Miscanthus sacchariflorus* and *Phragmites australis* over time in litterbags with mesh sizes of 1 mm (**a**, **c**) and 5 mm (**b**, **d**; mean±1 SD, n=3 or 4)

respectively. These rose over 263 days to 16–20 and 16–18 mg g^{-1}, respectively.

We previously recorded initial N concentrations of 6–7 and 24–28 mg g^{-1}, respectively, for *M. sacchariflorus* and *P. australis*, which then, over 204 days, changed to 10–12 and 16–17 mg g^{-1} (Kim et al. 2006). These differences demonstrate the influence of *H. japonicus* when it smothered those other two species versus their response to natural withering.

If plant-nitrogen levels are not sufficient to support microbial activity, N becomes a critical factor that slows decomposition (Smith and Smith 2001). *P. australis* and *Carex utriculata* both decay faster when N concentrations are elevated (Chamie and Richardson 1978; Polunin 1982). Here, N levels and moisture contents in both species were high enough for microbes and mineralization to begin. In the first 60 days, the remaining nitrogen within *M. sacchariflorus* and *P. australis* was significantly decreased to 47–50% and 48–51%, respectively, before decreasing more slowly throughout the rest of our study period (Table 2). Although earlier reports have stated that immobilization occurs after 3 months in *P. australis* (Mun et al. 2000) and that nitrogen levels can rise over the long term (Anderson 1973; Gholz et al. 1985; Kelly and Beauchamp 1987), we found no increase or immobilization of nitrogen here because the initial concentration was adequate for microbes.

Phosphorus concentrations within *M. sacchariflorus* and *P. australis* were 0.32–0.34 and 0.24–0.31 mg g^{-1} on day 0, respectively, and fluctuated early around those values. However, about 50% of the P in those species disappeared over 60 days (Table 2), with this loss being faster during the early phase of decomposition compared with values reported from other studies (Boyd 1970; Mason and Bryant 1975).

Initial Na concentrations for *M. sacchariflorus* and *P. australis* were 0.30–0.31 and 0.50–0.29 mg g^{-1}, respectively, versus 0.42 and 0.28–0.47 mg g^{-1}, respectively, at the end of study (Table 2). The remaining sodium within *M. sacchariflorus* decreased over 60 days to 57% and 30% in the 1- and 5-mm litterbags, respectively. This compared with declines over 108 days to 82% and 40% in 1- and 5-mm litterbags, respectively, for sodium within *P. australis*.

Calcium concentrations within *M. sacchariflorus* and *P. australis* were initially 25.5–27.2 and 33.2–41.5 mg g^{-1}, respectively, increasing over 263 days to 85–140 and 74–126 mg g^{-1}, respectively (Table 2). By the end of our study, the amounts of Ca remaining in *M. sacchariflorus* had risen to 230% and 145% in the 1- and 5-mm mesh litterbags, respectively, a result similar to what we reported previously (Kim et al. 2006). This confirmed that calcium does not leach out well (Planter 1970; Davis and van der Valk 1978; Mun et al. 2000).

Potassium levels in *M. sacchariflorus* and *P. australis* started at 164–166 and 178–208 mg g^{-1}, respectively,

Table 2 Changes in percentages of remaining mass and contents of N, C, P, Na, Ca, K, and Mg with incubation time

Plants	Elements	Time (days)						
		0	7	22	36	60	108	263
M. sacchariflorus in 1-mm mesh bag	Remaining mass (%)	100±21.7	90.4±7.2	67.5±6.8	56.0±12.8	57.3±0.7	48.9±9.8	43.6±4.1
	N (mg g^{-1})	13.9±1.03	11.6±1.23	14.2±1.65	14.1±3.67	14.4±1.08	17.3±1.19	19.9±2.69
	N (%)	100.0	78.0±6.34	61.9±5.12	55.1±9.55	50.4±0.97	43.8±7.49	42.9±2.83
	C (%)[a]	43.8±0.24	43.8±0.29	42.3±0.85	41.5±1.86	42.6±0.27	43.0±0.32	40.1±0.55
	C (%)[b]	100.0	80.3±6.53	63.7±5.27	56.7±8.27	51.8±6.80	45.1±7.71	44.2±2.92
	P (mg g^{-1})	0.34±0.06	0.43±0.04	0.41±0.02	0.40±0.02	0.42±0.02	0.66±0.28	0.61±0.19
	P (%)	100.0	86.1±7.00	68.3±5.66	60.8±10.6	55.6±1.07	48.4±8.27	47.4±3.13
	Na (mg g^{-1})	0.30±0.03	0.39±0.03	0.36±0.08	0.56±0.07	0.33±0.02	0.45±0.09	0.42±0.05
	Na (%)	100.0	106±15.9	76.9±18.3	108±30.2	57.0±1.73	66.8±1.76	62.9±12.0
	Ca (mg g^{-1})	27.2±4.2	40.1±6.7	52.1±5.3	52.6±10.0	69.8±4.3	91.9±17.8	140±27.4
	Ca (%)	100.0	121±27.4	124±17.2	110±20.5	135±9.43	152±3.47	230±44.8
	K (mg g^{-1})	163.8±54.0	164.9±18.5	121.9±25.3	148.8±15.7	170.2±22.1	92.5±29.4	22.3±14.9
	K (%)	100.0	82.3±14.7	47.5±5.93	52.9±14.1	54.5±6.19	26.5±12.6	6.27±4.58
	Mg (mg g^{-1})	11.1±1.3	13.8±2.8	17.2±2.2	20.9±5.2	20.6±0.8	22.8±4.7	21.1±1.8
	Mg (%)	100.0	103±26.3	100±6.57	109±33.8	98.1±5.18	92.8±3.26	85.3±3.69
M. sacchariflorus in 5-mm mesh bag	Remaining mass (%)	100±5.1	93.6±7.8	66.8±23.8	65.8±11.3	53.6±1.4	51.2±0.3	48.0±16.2
	N (mg g^{-1})	13.0±0.59	12.8±0.92	16.6±3.68	16.6±3.57	17.3±3.86	16.0±1.93	16.0±1.06
	N (%)	100.0	92.8±15.0	56.8±20	51.6±18.8	47.5±3.96	47.7±0.38	45.2±15.4
	C (%)[a]	43.5±0.16	43.2±0.45	42.1±0.90	42.3±0.82	43.2±0.34	43.0±0.13	40.2±1.39
	C (%)[b]	100.0	95.6±15.4	58.5±20.6	53.1±15.8	48.9±9.34	56.0±9.35	69.0±7.92
	P (mg g^{-1})	0.32±0.04	0.45±0.03	0.43±0.04	0.52±0.10	0.47±0.03	0.43±0.00	0.45±0.03
	P (%)	100.0	102±16.5	62.7±22.0	57.0±20.8	52.4±4.37	52.7±0.42	49.9±17.0
	Na (mg g^{-1})	0.31±0.03	0.38±0.05	0.47±0.18	0.34±0.13	0.19±0.14	0.32±0.12	0.42±0.03
	Na (%)	100.0	123±26.1	87.4±24.0	60.1±27.9	30.4±23.1	52.9±20.3	64.8±17.9
	Ca (mg g^{-1})	25.5±2.2	33.5±3.6	59.4±9.5	59.6±11.5	33.2±29.1	64.1±15.7	84.8±6.4
	Ca (%)	100.0	118±10.4	125±22.2	116±36.2	87.6±25.5	117±29.7	145±41.6
	K (mg g^{-1})	166±44	158±42	109±44	63±45	41±14	46±26	26±10
	K (%)	100.0	90.6±13.6	38.2±15.4	19.6±14.3	12.7±4.89	14.1±7.96	6.93±0.99
	Mg (mg g^{-1})	8.6±0.5	11.2±1.0	14.9±2.8	9.6±7.0	3.8±4.8	11.7±1.8	15.1±2.5
	Mg (%)	100.0	97.4±9.17	76.6±14.1	40.4±29.7	17.5±22.1	52.7±8.31	62.2±11.6
P. australis in 1-mm mesh bag	Remaining mass (%)	100±13.2	95.0±4.9	72.5±3.2	68.8±9.4	55.3±7.3	53.7±3.4	52.0±0.3
	N (mg g^{-1})	20.5±3.26	15.7±0.93	14.5±0.67	14.7±0.97	14.1±2.50	14.3±0.71	15.6±0.81
	N (%)	100.0	80.95±3.99	63.55±3.42	62.074±8.92	51.31±6.28	51.2±3.64	51.0±0.77
	C (%)[a]	41.8±0.57	41.6±0.94	41.3±0.58	40.9±0.40	41.6±0.62	42.2±0.30	39.4±0.82
	C (%)[b]	100.0	83.3±4.10	65.4±3.52	63.9±7.71	52.8±0.81	52.7±3.75	58.8±5.30
	P (mg g^{-1})	0.24±0.02	0.22±0.04	0.19±0.01	0.24±0.03	0.28±0.04	0.22±0.03	0.24±0.07
	P (%)	100.0	89.4±4.40	70.2±3.78	68.5±9.85	56.7±6.94	56.5±4.02	56.3±0.85
	Na (mg g^{-1})	0.50±0.16	0.40±0.04	0.43±0.07	0.44±0.04	0.57±0.14	0.46±0.06	0.47±0.05
	Na (%)	100.0	114±15.0	95.5±20.3	95.6±17.3	103±35.3	82.4±16.6	82.3±10.2
	Ca (mg g^{-1})	33.2±16.1	45.7±4.1	49.4±1.6	49.1±6.4	54.9±4.9	54.2±3.1	73.9±2.4
	Ca (%)	100.0	142±14.7	121±7.22	115±4.65	108±19.6	107±13.6	145±6.73
	K (mg g^{-1})	208±57	194±15	168±17	152±45	140±32	116±35	66±10
	K (%)	100.0	99.7±3.39	67.8±7.22	61.2±24.2	46.3±14.4	38.2±14.1	21.4±3.49
	Mg (mg g^{-1})	8.6±2.7	11.0±0.3	12.0±1.7	11.9±0.3	13.4±1.4	12.2±0.9	13.2±1.6
	Mg (%)	100.0	84.3±2.88	72.4±13.9	70.0±11.9	64.4±7.37	59.2±8.58	63.4±8.09
P. australis in 5-mm mesh bag	Remaining mass (%)	100±3.5	86.0±7.9	61.2±6.7	52.2±9.1	38.7±7.0	34.6±2.7	32.2±1.1
	N (mg g^{-1})	20.0±2.59	15.8±1.91	17.2±2.75	16.7±1.32	14.5±1.48	14.9±6.96	18.2±1.92

Table 2 (continued)

Plants	Elements	Time (days)						
		0	7	22	36	60	108	263
	N (%)	100.0	89.9±9.52	66.2±7.98	60.6±10.1	48.5±8.93	46.3±4.61	62.7±13
	C (%)[a]	43.2±0.40	41.7±0.35	40.1±2.16	41.3±0.20	41.4±0.99	42.6±0.83	40.2±0.50
	C (%)[b]	100.0	92.6±9.80	68.1±8.21	62.4±13.1	49.9±8.51	47.7±4.75	64.5±13.4
	P (mg g^{-1})	0.31±0.07	0.39±0.06	0.40±0.07	0.40±0.10	0.39±0.01	0.36±0.04	0.32±0.02
	P (%)	100.0	99.3±10.5	73.1±8.81	66.9±11.2	53.5±9.87	51.2±5.09	69.2±14.4
	Na (mg g^{-1})	0.29±0.03	0.36±0.02	0.40±0.09	0.35±0.09	0.31±0.05	0.25±0.00	0.28±0.03
	Na (%)	100.0	113±14.3	93.4±30.7	74.5±32.9	52.1±12.7	39.6±3.36	60.2±13.7
	Ca (mg g^{-1})	41.5±3.7	55.2±3.0	60.7±7.1	76.8±15.4	72.3±10.4	101±2.9	126±2.8
	Ca (%)	100.0	190±24.2	153±6.23	177±35.2	132±6.38	179±12.7	301±57.2
	K (mg g^{-1})	178±28.4	160±12.2	162±32.7	106±10.9	134±13.3	69.1±7.80	20.0±6.5
	K (%)	100.0	91.4±5.25	67.1±7.76	41.2±11.0	41.9±11.7	20.3±0.27	8.24±4.14
	Mg (mg g^{-1})	10.4±0.5	11.1±1.4	17.1±2.5	15.3±0.5	11.6±1.7	14.9±0.1	16.4±2.3
	Mg (%)	100.0	93.2±3.58	108±27.1	87.1±11.7	53.1±10.9	65.1±7.09	95.5±11.5

[a] Concentration

[b] Remaining percentage

dropping to 22–26 and 20–66 mg g^{-1}, respectively, by the end of the study period (Table 2). The amount of K remaining in *M. sacchariflorus* was 6% and 7% in the 1- and 5-mm litterbags, respectively, when our observations were completed. For *P. australis*, K concentrations in materials from the 1- and 5-mm litterbags declined by 21% and 8%, respectively, and no immobilization was detected. In aquatic macrophytes, the disappearance of potassium occurs rapidly within the first 2 weeks (Brinson 1977). Nevertheless, although this study focused on plants growing beneath *H. japonicus*, rather than in the water, we also noted that the amounts of remaining K declined within 3 weeks, to 38–48% (*M. sacchariflorus*) and to 67–68% (*P. australis*) in our 1- and 5-mm litterbags, respectively (Table 2).

Magnesium concentrations were initially 8.6–11.0 in *M. sacchariflorus* and 8.6–10.0 mg g^{-1} in *P. australis*. These levels changed continuously over 263 days, becoming 15–21 and 13–16 mg g^{-1}, respectively (Table 2). Remaining values decreased respectively to 85% and 62% in the 1- and 5-mm mesh litterbags for *M. sacchariflorus* and to 63% and 53% for *P. australis*. Berg and Laskowski (2006) have reported that this decline in Mg stops at a certain concentration before slowly rising as decomposition proceeds. Likewise, here, we found that amounts of magnesium also dropped in the first 60 days and then slowly increased.

Emergent hydrophytes lose K, Mg, and P during the first month of decomposition (Mason and Bryant 1975); this phenomenon was also noted with K and P in our current study. However, values for Mg were not as stable as those we had previously calculated (Kim et al. 2006). In general, Na and K were easily leached, Ca and Mg were more recalcitrant (see Kim et al. 2006), K levels decreased the most, and Mg the least among all cations.

Based on our results, we could identify the five main factors that contributed to the rapid decomposition in August of *M. sacchariflorus* and *P. australis* that had been smothered by *H. japonicus*. First, appropriate plant C:N ratios are necessary for the activation of microbes—here, those values were suitable at 15–30, thereby accelerating decomposition rates. Second, high moisture contents in these plants enabled microbial growth and faster decay. Third, high plant-nutrient levels are associated with greater losses of mass inside litterbags (Davis and van der Valk 1978; Berg et al. 1982). We also noted a positive correlation between initial N/P contents and rates of mass decline. There was no time for nutrients to be translocated within *M. sacchariflorus* and *P. australis* before those fallen plants were decomposed. Fourth, the relative light intensity was low, i.e., 4.76%, in areas that were 100% shaded by *H. japonicus*. This was compared with intensities of 9.75% under 80% coverage by *P. australis* and 16.9% when that species covered 40% of the area (unpublished data). Therefore, under such dark conditions, microbes and invertebrates were able to thrive without becoming desiccated among *Humulus*-shaded plants with high nutrient contents. Finally, humidity and temperature remained high and stable in the microclimate produced by *Humulus*, thus promoting microbial activity and increasing decomposition rates (see also Swift et al. 1979).

Average annual productivity by these *M. sacchariflorus* and *P. australis* communities was 929 and 640 g, respec-

tively, at Amsa-dong (unpublished data) and 1,865 and 1,179 g on Bam-Sum Island and in the Godug-dong ecosystem preservation area (Seoul City 2003, 2005). If the overtopped *M. sacchariflorus* decomposed over a 60-day period, then 5,560 (N) and 137 mg m^{-2} (P) would be returned to the soil and could be used by *H. japonicus* until October when that species stopped its growth and seed production (Ju et al. 2006). In a *P. australis* community, 6,864 (N) and 91 mg m^{-2} (P) would have returned to the soil in that 60 days. Therefore, growth of the *H. japonicus* plants would have been enhanced by the rapid decomposition of those other species because of elevated amounts of available soil nutrients.

Conclusion

Annual decay rates for *Humulus*-shaded *M. sacchariflorus* (1.61–1.74) and *P. australis* (1.46–3.54) were higher than for those respective plants that withered naturally (0.57–1.83 and 0.02–1.18). This demonstrates that *H. japonicus* accelerated the decomposition of both species and also activated such decay earlier in the year, i.e., in August. Nutrient cycling was elevated in the presence of *Humulus*, a result of the low C/N ratio, high moisture content, greater amounts of N and P in the decaying plants, and an improved environment for decomposition due to a lower light intensity and a higher and more stable humidity and temperature. All of these factors enabled *H. japonicus* to grow quickly, thereby accelerating nutrient cycling in these riverine wetlands.

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